PSYCHE 91, 1984 171-192
("1984")

CAMBRIDGE ENTOMOLOGICAL CLUB

OFFICERS FOR 1984–1985

President ..... M. DEANE BOWERS
Vice-President ..... WAYNE MADDISON
Secretary ..... ARDIS JOHNSTON
Treasurer ..... FRANK M. CARPENTER
Executive Committee ..... BARBARA L. THORNE
NORMAN F. CARLIN

EDITORIAL BOARD OF PSYCHE

F. M. CARPENTER, (Editor), *Fisher Professor of Natural History, Emeritus, Harvard University*
W. L. BROWN, JR., *Professor of Entomology, Cornell University and Associate in Entomology, Museum of Comparative Zoology*
B. K. HÖLLDOBLER, *Professor of Biology, Harvard University*
H. W. LEVI, *Alexander Agassiz Professor of Zoology, Harvard University*
M. D. BOWERS, *Assistant Professor of Biology, Harvard University*
ALFRED F. NEWTON, JR., *Curatorial Associate in Entomology, Harvard University*
E. O. WILSON, *Baird Professor of Science, Harvard University*
J. M. CARPENTER, *Assistant Professor of Biology, Harvard University*

PSYCHE is published quarterly by the Cambridge Entomological Club, the issues appearing in March, June, September and December. Subscription price, per year, payable in advance: $15.00, domestic and foreign. Single copies, $4.00

Checks and remittances should be addressed to Treasurer, Cambridge Entomological Club, 16 Divinity Avenue, Cambridge, Mass. 02138.

Orders for missing numbers, notices of change of address, etc., should be sent to the Editorial Office of Psyche, 16 Divinity Avenue, Cambridge, Mass. 02138. For previous volumes, see notice on inside back cover.

IMPORTANT NOTICE TO CONTRIBUTORS

Manuscripts intended for publication should be addressed to Professor F. M. Carpenter, Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

Authors are required to bear part of the printing costs, at the rate of $29.00 per printed page. The actual cost of preparing cuts for all illustrations must be borne by contributors: the cost for full page plates from line drawings is ordinarily $10.00 each, and for full page half-tones, $12.00 each; smaller sizes in proportion. There is ordinarily no additional charge for setting tables of less than six columns; for tables of six or more columns the cost is $25.00 per page.

Psyche, vol. 91, no. 1-2, for 1984, was mailed November 15, 1984

The Lexington Press, Inc., Lexington, Massachusetts

RECORDED
IN ANTBIB

Wheeler, D.E. 1985 (1984)
[22 April 1985]

PSYCHE

Vol. 91 1984 No. 3-4

BEHAVIOR OF THE ANT, *PROCRYPTOCERUS SCABRIUSCULUS* (HYMENOPTERA: FORMICIDAE), WITH COMPARISONS TO OTHER CEPHALOTINES

By Diana E. Wheeler

Smithsonian Tropical Research Institute
Apartado 2072, Balboa, Republic of Panama
and
*Museum of Comparative Zoology Laboratories
Harvard University, 26 Oxford Street
Cambridge, Massachusetts 02138

INTRODUCTION

Cephalotini is a well-defined tribe of Neotropical, arboreal ants of exceptional appearance, containing about 110 species in 4 genera (Kempf, 1973). Cephalotines can be distinguished from all other ants on the basis of the proventricular valves, which are sclerotized and shaped somewhat like the head of a mushroom (Emery, 1888; Kempf, 1951). The unusually thick exoskeleton bears generous sculpturing that can include numerous striations, ridges, and flanges, as well as protective spines. The four genera have an unusually complete array of worker caste systems for such a small tribe. The genus *Procryptocerus,* containing 28 species, is typically monomorphic. *Eucryptocerus* also has a monomorphic worker caste, but contains only 3 rare species. In *Cephalotes,* workers typically have a wide size range, and in *Zacryptocerus,* worker castes range from polymorphic to dimorphic and include the most highly modified soldier forms (Kempf, 1951, 1973).

*Address for correspondence
Manuscript received by the editor May 16, 1984

The behavior of *Cephalotes atratus* (Corn, 1980) and *Zacryptocerus varians* (Wilson, 1976; Cole, 1980) have been examined in detail. Both Wilson (1976) and Corn (1980) stressed the importance of studying the divergent genus *Procryptocerus* in order to factor out behaviors that are related to ecological peculiarities from those tied to the evolution of polymorphism within the tribe. Among cephalotines, *Procryptocerus* appears, at least superficially, most similar to typical myrmicine ants because the head and thorax lack elaborate spines and flanges. Further, since the worker caste is monomorphic, and therefore less complex than in other cephalotines, it has been assumed to be the most primitive genus of the tribe.

The species *P. scabriusculus* is found from Mexico to Venezuela (Kempf, 1972). It nests in dead wood, principally twigs, and forms polydomous, polygynous colonies. Here I present the results of a behavioral study on workers and queens of *P. scabriusculus* as a contribution towards understanding the biology of this species and the relationship between behavior and polymorphism within the Cephalotini.

METHODS

Nests of *P. scabriusculus* were collected in Escazu, near San Jose, Costa Rica. Three clusters of inhabited twigs were taken in late August, 1983, from *Spondias purpurea*. The colony observed in this study was extracted from 3 closely spaced dead twigs and presumed to be a major part of a single colony. It contained 6 queens, 62 workers, 10 worker pupae, 1 male pupa, 49 larvae, and 27 eggs. Both trophic and normal eggs were present. One additional colony was collected in a fig tree in November, 1982.

The observation nest was a 100 × 15 mm plastic petri dish. A small test tube, containing water held back by a cotton plug, was placed in the center of the dish to provide moisture and a nest site. The petri dish fit easily on the stage of a dissecting microscope. Observations used for the ethogram were made over a period of 7 days. During this period, the colony was supplied with diluted honey and dead insects. The honey was quickly consumed by workers, but the insects were rarely touched. Occasionally, workers appeared to be drinking the body fluids of freshly killed insects. The colony was observed for a total of 20 hours, in 40 30-minute observation periods. During each 30 minute period, the nest was scanned

every 2 minutes. Therefore, if an act lasted 30 minutes, it would be recorded 15 times.

Most of the periods of observation fell between 0900 and 2300, but ants were also watched at 0200, 0400, and 0600. The colony was exposed to light from dawn (0500) until room lights were turned off (2100–0200). Under these conditions, the colony was arrhythmic; no regular differences in activity levels or types of behaviors were noted. Pupal to adult molts took place at different times of day and night. Molting is strictly tied to the biological clock in many insects, and the fact the molting was irregular suggests that the colony was physiologically, as well as behaviorally, arrhythmic.

The behavioral repertoire was analyzed using a FORTRAN program written by R. Fagen for catalogue analysis using a log normal fitting procedure developed by Bulmer (1974) (Fagen and Goldman, 1977; Fagen, 1978).

Colonies of *Zacryptocerus minutus* and *Z. christopherseni* were collected in central Panama. Various observations are reported here for comparison with the biology of *P. scabriusculus.*

RESULTS

CHARACTERIZATION OF THE FEMALE CASTES

Two characteristics of the genus *Procryptocerus* are that the worker caste is monomorphic and that queens are slightly larger but very similar to workers (Kempf, 1951). The 2 female castes are compared graphically in Figure 1, in which head width is plotted against thoracic width. The size range of workers is so narrow that this caste can be considered monomorphic. Head widths of *P. scabriusculus* workers ranged from 1.14–1.36 mm, a difference of only 0.22 mm. This is trivial in comparison to *Z. minutus* (0.96–1.7 mm) and *Z. christopherseni* (1.42–2.66 mm), 2 species with distinct soldiers. In *C. atratus* workers, head width across the occipital spines ranged from about 2–4.5 mm (Corn, 1980).

Queens are morphologically similar to workers, but can be distinguished from workers on the basis of a variety of quantitative as well as discrete differences. As shown in Fig. 1, queens can be distinguished from workers on the basis of thoracic width. Other characters that are caste-specific are abdomen width and length, thoracic morphology, including wing scars, and the presence of ocelli.

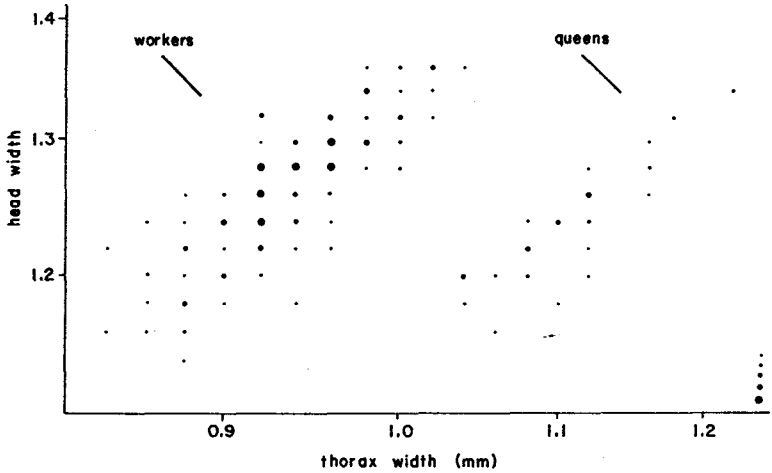

Fig. 1. Bivariate plot of morphological measurements for workers and queens. Size of filled circles indicates, in order of increasing size, 1, 2, 3, 4, and 5 or more individuals. Workers: n=136, slope=0.74, correlation=0.82. Queens: n=33, slope=0.77, correlation=0.89. Data are from two colonies.

WORKERS

A total of 6823 behavioral acts were performed by workers and recorded over a period of 20 hours. These are presented by category in Table 1. Workers performed 31 types of acts, and, using the methods of Fagen and Goldman (1977), and Bulmer (1974), a true repertoire size of 31 was estimated. The range of the 95% confidence interval was less than 1 act. It must be emphasized that this level of accuracy applies only to the context in which the ants were observed. Undoubtedly, other behaviors would be expressed under other conditions, such as attack. Also, behaviors that are very rare or that are partially suppressed under laboratory conditions may not be recorded. Egg laying, for example, was not observed during this study. The following worker behaviors listed in Table 1 are treated in greater detail below: abdominal trophallaxis, transfer of liquid food (=regurgitation, oral trophallaxis), self-grooming, fate of infrabuccal pellets, excavating, and antennal tipping. In addition, several behaviors not included in the ethogram are discussed: stridulation, defense, and miscellaneous leg movements.

Abdominal trophallaxis

Both Wilson (1976) and Cole (1980) found that *Z. varians* exhibited a behavior rarely found in ants, abdominal trophallaxis. This behavior has not been observed in the only other cephalotine previously studied, *C. atratus* (Corn, 1980). Here I report that *P. scabriusculus* also exhibits abdominal trophallaxis. The behavior was observed primarily in individuals that had just emerged. Within hours after a worker eclosed and was able to walk, it initiated abdominal trophallaxis, licking the abdominal tip of a nestmate. Single contacts lasted as long as 30 minutes, and the same individual engaged in additional, shorter contacts over a period of several hours. Brief periods of abdominal trophallaxis between older workers and between a worker and a queen was also observed. These contacts were much shorter than the contacts involving callows, generally less than 10 seconds and frequently only 1–2 seconds.

The function of this unusual ant behavior remains unknown. The fact that callows, newly molted individuals, seek out the substance is reminiscent of proctodeal feeding so well documented in lower termites (Cleveland, 1926). Such behavior would be appropriate for transferring essential gut flora to newly ecdysed adults. Finally, it is a suspicious coincidence that cephalotines have two unusual characters apparently associated with the digestive tract: the mushroom-shaped, sclerotized proventricular valves and abdominal trophallaxis. Perhaps these ants have undiscovered dietary peculiarities.

Outside the cephalotines, abdominal trophallaxis has been reported between the slavemaking ant, *Harpagoxenus americanus*, and its host species, *Leptothorax ambiguus* and *L. longispinosus*. Workers and queens of *H. americanus* occasionally assume a stereotyped posture, with the abdomen raised, and exude a droplet of fluid which is consumed by workers of the host species (Stuart, 1981). This unusual case of interspecific trophallaxis undoubtedly has an entirely different function than the type of abdominal trophallaxis described in cephalotines which occurs primarily between callow and fully pigmented workers.

Transfer of liquid food

Workers of *P. scabriusculus* exchange liquid food at moderately high rate in comparison other cephalotines. 15.9% of total acts performed by workers involved exchange (donating plus soliciting) of

Table 1. Behavioral repertoire of *Procryptocerus scabriusculus*. Number of acts and relative frequencies observed in 20 hours.

Acts	Workers	Queens
Self-groom		
antennae and legs	1945(.2851)	75(.2517)
abdomen and legs	86(.0126)	2(.0070)
lick abdominal tip	16(.0023)	
Antennal tipping	48(.0070)	
Abdominal trophallaxis		
callow licks worker	65(.0095)	
worker licks worker	26(.0038)	
worker licks queen	7(.0010)	
Solicit and or donate liquid food		
with worker	988(.1448)	99(.3322)
with queen	99(.0145)	16(.0537)
Solicit from larvae		93(.3110)
Infrabuccal pellets		
extrude	3(.0004)	
help nestmate extrude	3(.0004)	
carry	9(.0013)	
Allogroom		
worker	1036(.1518)	4(.0134)
queen	257(.0377)	1(.0034)
Eat		
egg	75(.0110)	6(.0201)
larva or pupa	97(.0142)	
unidentified brood	13(.0019)	
honey	23(.0034)	
Lick		
egg	34(.0050)	
larva	308(.0451)	
pupa	206(.0302)	
lick molting pupa	44(.0064)	
new emergent	145(.0213)	
Manipulate, carry, drag		
egg	42(.0062)	
larva	68(.0100)	2(.0067)
pupa	17(.0025)	
callow	6(.0009)	
Excavate	908(.1331)	
Lick wall of nest	60(.0088)	

Table 1. (continued)

Acts	Workers	Queens
Debris		
carry, manipulate	178(.0261)	
lick	11(.0016)	
Total number of acts	6823(1.0000)	298(1.0000)

food with another adult ant. Since donating and begging are combined, the number must be halved to be compared to the "regurgitation with" category reported in other behavioral repertoires. This figure (8.0%) is higher than in *C. atratus*, where donating made up about less than 2% of worker acts (Corn, 1980). It is much lower than the relative frequency of exchange found in *Z. varians* by both Wilson (1976) and Cole (1980), 22.8% and 21.3% respectively, as the rate of regurgitation in minor workers. *Z. varians* soldiers have a more limited repertoire than minor workers and devote over 40% of their behavioral acts to exchange of liquid food (Wilson, 1976; Cole, 1980).

The relative frequency of exchanging liquid food in *P. scabriusculus* is moderately high in comparison to other myrmicine ants. *Pogonomyrmex badius* lacks the behavior entirely (Wilson and Fagen, 1974). In *Orectognathus versicolor*, an advanced dacetine, relative frequency of oral trophallaxis is low, between 1 and 2%, in all worker size classes (Carlin, 1981). *Leptothorax curvispinosis* (5–10%) and *L. duloticus* (4–6%) (Wilson and Fagen, 1974; Wilson, 1975), have relative frequencies similar to *P. scabriusculus*.

Self grooming

A notable feature of self-grooming in *P. scabriusculus*, compared to that of other cephalotines studied, is that abdominal self-grooming movements are performed. In workers, about 4% of all self-grooming acts involved abdominal grooming with the fore- or hind legs. The abdomen was tucked under somewhat to facilitate complete coverage. In addition, in about 1% of self-grooming acts, the abdomen was bent forward between the legs and the tip licked. Self-grooming of the abdomen has never been observed in either *C. atratus* or *Z. varians* (Wilson, 1976; Cole, 1980; Corn, 1980). The

fact that *P. scabriusculus* was able to perform this maneuver demonstrates that the loss of abdominal grooming in other cephalotines was not related to the inflexibility conferred by heavy armor. Of greater significance, the ability to autogroom the abdomen, especially the tip, casts doubt on a suggestion made by Wilson (1976) and echoed by Cole (1980) that the acquisition of abdominal trophallaxis by cephalotines was tied to loss of maneuverability.

Fate of infrabuccal pellets

P. scabriusculus workers regurgitated infrabuccal pellets and the action frequently attracted the interest of a nestmate. However, ants never ate the pellets or offered them to larvae, as has been observed in *Z. varians* (Wilson, 1976; Cole, 1980). As soon as a pellet was regurgitated, a worker would leave the brood area and drop the pellet onto the floor of the petri dish. Regurgitation of infrabuccal pellets was never observed in *C. atratus* (Corn, 1976).

Excavation

Usually several workers were at the rear of the nest tube digging at the damp cotton with their legs and mandibles. Presumably this behavior would be homologous to excavating the blind end of a tunnel in a twig nest.

Antennal tipping

A stretching behavior dubbed antennal tipping by Wilson and Fagen (1974) was frequently observed. This behavior has been noted in many ant species, including *Leptothorax curvispinosis, L. duloticus* (Wilson, 1975), *Formica perpilosa* (Brandao, 1978), *Colobopsis* sp. (Cole, 1980), *C. atratus* (Corn, 1980) and *Z. varians* (Wilson, 1976; Cole, 1980). In *P. scabriusculus*, the first pair of legs were extended forward and the rear 2 pairs extended backwards. The body was elevated due to the leg extension and the abdomen drooped slightly. The position of the head was more variable. Sometimes it was raised and sometimes it was tucked under the body. The impression was one of rigidity, and the body sometimes trembled slightly or the antennae vibrated.

Stridulation

Both workers and queens stridulated when physically trapped or restrained. This behavior does not appear in the behavioral reper-

toire (Table 1) since it was produced only when ants were held and not under the standard conditions for observation. When an ant was provoked into stridulating, nearby nestmates did not obviously alter their behavior. The stridulatory file is located on the neck of the gaster where it inserts into the post-petiole.

The presence and use of a stridulatory organ in *Procryptocerus* is remarkable as it is found in no other genus of cephalotines. The absence of a stridulatory organ in the Myrmicinae is unusual; Markl (1973), in a survey of stridulatory structures in ants, found that 83% of myrmicine genera had them. So, it is intriguing first, that most cephalotines have lost the file and second, that *Procryptocerus* has retained the structure. Markl (1973) found the stridulatory organ in all 7 species of *Procryptocerus* he examined.

Four subfamilies of ants have stridulatory organs: the Nothomyrmeciinae, the Pseudomyrmicinae, the Ponerinae and the Myrmicinae (Sharp, 1893; Haskins and Enzmann, 1938; Markl, 1973; Taylor, 1978). The stidulatory organ is always found on the same pair of segments: the file is located on abdominal segment IV and the scraper on segment III. In view of the apparent evolutionary stability of the stridulatory organ's position, its presence in *Procryptocerus* can be regarded as a reliable primitive character.

The ability to stridulate is common in ants, but the role of stridulation in communication has been demonstrated in only two cases. Markl (1965) showed that stridulation serves as a distress signal in *Atta cephalotes*. Buried workers stridulate and nestmates respond by digging in the vicinity of the sound. Markl and Hölldobler (1978) have shown that in *Novomessor*, stridulatory signals function as a mechanism for modulating responses to other stimuli. For example, food retrieving behavior was enhanced when chemical recruitment stimuli were received concurrently with stridulatory signals. *Novomessor* stridulates spontaneously, without the provocation of physical restraint.

Neither of these proven roles of stridulation applies directly to *P. scabriusculus*. Digging is not an appropriate rescue response in an arboreal nest, and the fact that *P. scabriusculus* does not stridulate spontaneously, without restraint, argues against an analogy with *Novomessor*. A third possibility is that stridulatory vibrations deter predators. This phenomenon has been documented in insects other than ants (see Masters, 1979).

Defense

P. scabriusculus relies almost exclusively on its thick exoskeleton, with cephalic scrobes to shield the antennae, to discourage enemies and predators. In response to real or supposed threats (other ants, freshly killed flies, seeds, flowers, pollen, etc.), workers lowered their heads, contacted the object, and pushed. The workers also nipped as best they could with their small, blunt mandibles. *P. scabriusculus* was ineffective in coping with enemy ants in the open. One colony in a petri dish took 12 hours to clip the legs off a *Pseudomyrmex* sp. worker placed in the nest. Presumably bulldozing would be more effective inside a twig nest in preventing trespassers from entering and nipping would be more effective where the enemy could be pinned against the walls of the narrow passageways.

Leg movements

Another behavior not included in the repertoire is miscellaneous leg movement. When ants were inactive, standing quietly in position, often 1, 2, or, rarely, 3 of their legs might be moving. Most of the movement was made by the tibia and tarsus, which were swung as a unit, while the femur stayed in place. Often, the femur was flexed and also participated in the movement. About 60% of the time the movement involved one of the rear legs, 30% a middle leg, and 10% a front leg. The behavior was observed in queens as well as workers.

QUEENS

Number of queens

P. scabriusculus has multiple queens. The colony observed in this study contained, at the time of collection, 6 dealate queens and 62 workers (8.8% queens). After the study was terminated, the colony was preserved in alcohol. Subsequent dissection showed that all 6 queens had fully developed ovaries. In addition, 3 queens (#1, #4, and #6) contained at least one egg large enough to fall in the size range of viable eggs. Two fragments of other colonies contained 4 queens with 40 workers (9.1%) and 1 queen with 17 workers (5.5%). A large colony collected in November, 1982, contained 72 workers with 27 queens (27%). In this colony, many of the queens had unexpanded, crumpled wings indicating that they had been produced within the colony and were not primary, founding queens.

In ants, polygyny evolves under special ecological conditions, such as short-lived nest sites (Hölldobler and Wilson, 1977). Therefore, it is not a reliable indicator of major phylogenetic trends within a group. Apparent polygyny (the presence of multiple dealate queens) is scattered throughout the advanced genus *Zacryptocerus*. In *Z. texanus*, Creighton and Gregg (1954) (see also Creighton, 1963; Creighton, 1967) found colonies and colony fragments containing 0–14.7% queens. In *Z. christopherseni*, I found 13 dealate queens in a single colony containing over 4,000 workers and soldiers. In contrast, *Z. rowheri* (Creighton and Nutting, 1965), *Z. pusillus* (Limongi, 1977), *Z. varians* (Wilson, 1976), *Z. minutus* (personal observation), as well as *Cephalotes atratus* (Corn, 1980) and *Eucryptocerus placidus* (Corn, 1976) are apparently monogynous.

Behavior of queens

Queens performed a total of 298 acts in 9 categories over a period of 20 hours (Table 1). When data were fitted to a lognormal Poisson distribution (Fagen and Goldman, 1977), the true repertoire size of queens in a laboratory nest was estimated to be 11, with a 95% confidence interval of ±3, types of acts.

The entire repertoire of queens, with the exception of self-grooming, was devoted to eating. Queens solicited and received food not only from workers but also from larvae. Queens used antennal soliciting movements and licked larvae vigorously around the mouth to demand food. This behavior is similar to that described for queens of *Leptothorax curvispinosus*, which solicit labial gland secretions from larvae (Wilson, 1974).

Most of the queens' infrequent behaviors, shown in Table 1, were probably associated with behavioral sequences leading up to demanding food from workers or larvae. For example, grooming of workers preceded solicitation movements with the antennae. Manipulation of larvae, moving them into a better position, was a prelude to solicitation behavior.

P. scabriusculus queens, which performed acts in 9 behavioral categories, were more versatile than queens of *Z. varians*. In *Z. varians*, queens performed only 3 acts: self-grooming, regurgitating with minor workers, and laying eggs (Wilson, 1976; Cole, 1980). Outside the Cephalotini, 5 repertoires of queens are available. Repertoire size ranges from 5 in *Colobopsis* sp. (Cole, 1980) and

Leptothorax curvispinosus (Wilson and Fagen, 1974) to 8 in *Orectognathus versicolor* (Carlin, 1981), 9 in the slavemaking species, *Leptothorax duloticus* (Wilson and Fagen, 1974), and 16 in the primitive ponerine, *Amblyopone pallipes* (Traniello, 1982). In respect to other ant species, then, the repertoire size of *P. scabriusculus* queens appears to be average. In comparison to the queen of *Z. varians*, however, the queen of *P. scabriusculus* is much less behaviorally specialized.

Variation in behavior of individual queens

To determine if there were differences in the behavior of individual queens that might reflect reproductive dominance, queens were marked with colored paint and the acts of each recorded for 15.5 hours of the study. The most common acts in which queens participated were soliciting liquid food from workers, soliciting liquid food from larvae, self-grooming movements, and being groomed by a worker (Table 2). For comparison, the average number of similar acts recorded for workers during the same 15.5 hour period is also shown in Table 2.

The 6 queens showed considerable variation in their rates of soliciting liquid food. A chi-square test showed that pattern of queen behavior was significantly different from an even distribution for both soliciting food from workers ($p<0.025$) and soliciting food from larvae ($p<0.005$). The amount of food that queens were able to collect from workers and larvae could be directly associated with rank, the amount being an indication of resources convertible to

Table 2. Behavior of individual queens. Values given are actual numbers of acts in a category that were performed by each individual in 15.5 hours of observation. The average queen values are means of acts performed by the six queens. The value for average worker is the number of acts in a category performed by workers in 15.5 hours of observation divided by the number of workers (n=62). Queens solicited from larva by antennating and licking larvae around the mouth. Workers licked larvae as part of brood care and did not concentrate in the head region. Values of p for differences among queens were determined using a chi-squared test.

Queen #	1	2	3	4	5	6	av. queen	av. worker	p
Solicit from worker	13	16	5	23	9	11	13	7	<.025
Solicit from/lick larva	7	12	7	25	13	10	12	4	<.005
Self-groom	12	10	12	4	8	2	8	25	<.005
Groomed by worker	26	39	40	35	43	31	36	15	ns

viable eggs. In soliciting, queen #4 clearly led all the rest, while queen #3 was the clear loser. The least demanding queens participated in food exchange with workers at a rate similar to workers: such queens can be regarded as worker-like in their behavior (Table 2).

Occasionally, queens solicited from other queens (n=9). One queen would initiate the contact, but both would perform soliciting movements with their antennae. No food appeared to be exchanged during these bouts. The number of queen-queen contacts was not directly correlated with rank as determined by rates of queen-worker and queen-larvae exchanges. The sample size is so low, however, that it is premature to dismiss the possibility that rank is determined or maintained by such interactions.

The relationship between grooming patterns and rank, if one exists, is not clear (Table 2). There were significant differences among queens in the amount of self-grooming indulged in ($p<0.005$, chi-squared test), but the difference in attention received from workers was not significant. Queens groomed themselves less than the average worker and were groomed by workers more often than workers groomed each other. No queen could be classed as worker-like in grooming behavior.

Viable and trophic eggs

Both normal, viable eggs and trophic eggs are found in *P. scabriusculus* colonies. Viable eggs in *P. scabriusculus*, those capable of embryogenesis, were large and cylindrical, measuring 1.32–1.66 mm long. The shape is typical of Cephalotini, as well as other arboreal ants (Wheeler and Wheeler, 1954). Smaller, presumably trophic, eggs were highly variable in size (0.6–1.2 mm). Trophic eggs were less cylindrical than viable eggs and had a milky, homogeneous appearance. Generally, ants consume trophic eggs immediately after they are laid (Wilson, 1971). Why *P. scabriusculus* should allow non-viable eggs to lie around is a puzzle.

The relative capabilites of egg laying in workers and in queens is not known, since no egg laying was observed. In other cephalotines, workers are known to lay trophic eggs as well as viable, unfertilized eggs that develop as males. In *Z. varians*, minor workers lay trophic eggs (Wilson, 1976), and production of males by queenless colonies has been noted in *C. atratus* (Weber, 1957), *Z. varians* (Wilson, 1976) and *Z. minutus* (personal observation).

Discussion

Can a comparison of behaviors within the Cephalotini contribute to an understanding of the phylogeny within the tribe or of the evolution of morphological worker castes? Including the behavioral data reported here, information is available for the three major genera of cephalotines: *Procryptocerus, Cephalotes, and Zacryptocerus.* It is now possible to compare and integrate behavioral with morphological data in considering phylogenetic relationships among cephalotines.

Only behavioral characters that do not occur in all members of a group can be useful in constructing alternative paths of evolution. Six such characters known for three species of cephalotines are listed in Table 3. First, I will use these characters to illustrate overall behavioral similarities between species. Then, the polarity (ancestral vs. derived state) of these characters will be surmised and used to construct behavioral cladograms (Fig. 2). Finally, the evolutionary relationships suggested by the cladogram can be used to re-examine our assumptions about the evolution within the cephalotines and their diverse morphological worker castes.

P. scabriusculus has been characterized as morphologically divergent (Kempf, 1951), quite discrepant (Kempf, 1973), and primitive (Corn, 1976; Wilson, 1976). In its behavior, however, it shares a remarkable number of traits with the advanced species, *Z. varians* (Table 3). Table 3 indicates that *P. scabriusculus and Z. varians* share four of the six discrete behavioral characters listed, two of

Table 3. Comparison of behavioral characters among three cephalotine species, representing the three major genera. The six behaviors that are listed may have phylogenetic significance. An asterisk (*) indicates which behavioral state is considered derived. Note that *Procryptocerus scabriusculus* and *Zacryptocerus varians* share four characters, while *Z. varians* and *Cephalotes atratus* share two. *P. scabrius-culus* and *C. atratus* share none of the six behavioral states. Abbreviations given are used in Figure 2.

	Cephalotes	*Zacryptocerus*	*Procryptocerus*
Abdominal trophallaxis (at)	no	(yes*	yes*)
Adult transport (car)	yes	(no*	no*)
Infrabuccal pellets	no*	(yes	yes)
Lay trophic eggs	no*	(yes	yes)
Stridulate (str)	(no*	no*)	yes
Abdominal self-groom (ag)	(no*	no*)	yes

which are primitive. *Z. varians* and *C. atratus* share only two characters, while *P. scabriusculus* and *C. atratus* share none. *P. scabriusculus* and *C. atratus* are both considered relatively primitive, but behaviorally they are primitive in different ways.

On the basis of morphological characters, Brown (1973) felt that all cephalotine genera besides *Procryptocerus* could be lumped. Kempf (1973) maintained the distinction betwen the genus *Cephalotes* and *Zacryptocerus*. The behavioral data show that *C. atratus* is divergent from both *P. scabriusculus* and *Z. varians* and therefore support the generic distinctions proposed by Kempf (1973).

The probable polarity (ancestral vs. derived state) of each of the characters in Table 3 can be assessed by outgroup comparisons with other ants. The closest relatives of the Cephalotini are, unfortu-

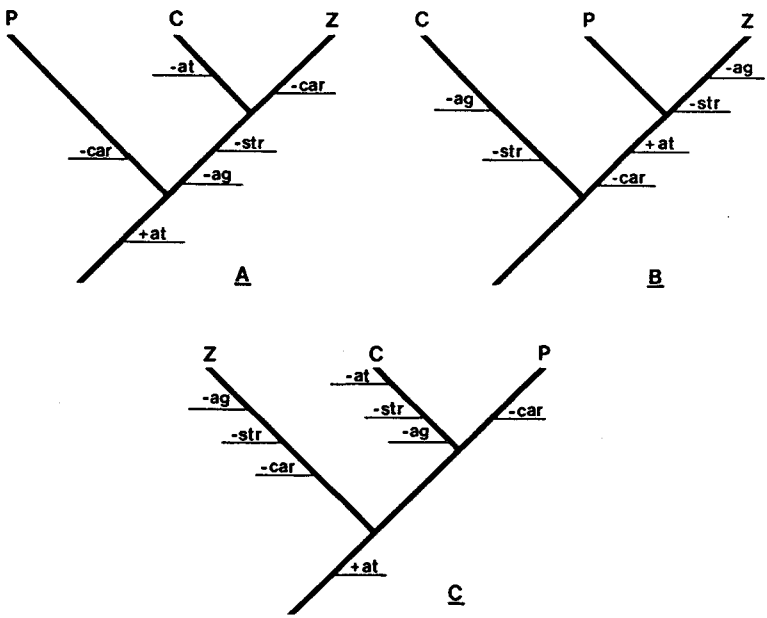

Fig. 2. Cladograms for 4 synapomorphic characters in 3 species of cephalotines: *Procryptocerus scabriusculus, Cepahlotes atratus,* and *Zacryptocerus varians.* The ancestral cephalotine is assumed to have had the following profile: −at (abdominal trophallaxis), +ag (abdominal grooming), +str (stridulation), +car (adult transport =carrying nestmate).

nately, not known. Therefore, cephalotines are compared with other myrmicines, when that information is available, as well as with other subfamilies. Two important behaviors, abdominal trophallaxis and stridulation (see Table 3), were discussed in detail above. Adult transport, in which one adult carries another, occurs widely in ants, and is especially well developed and stereotyped in the Myrmicinae and the Formicinae (Wilson, 1971; Möglich and Hölldobler, 1974). Therefore, the expression of this behavior is considered the primitive condition in the Myrmicinae and its loss the derived state.

Behavioral Cladograms

Cladograms provide a useful device for examining possible ways different sets of characters could have evolved. I will assume that the three species, *P. scabriusculus*, *C. atratus*, and *Z. varians*, are monophyletic, *sensu* Hennig (1966); no species is an ancestor of either of the others. I also assume that the three species involved are representative of their genera. Recognizing that this second assumption may be premature, I stress that more species need to be studied, especially in the diverse genus *Zacryptocerus*.

The most useful characters in constructing cladograms are those that are synapomorphic, derived traits that are shared. There are three ways that three species could have evolved such that two now share an advanced trait. The simplest is that the two species share a common ancestor that possessed the character. The second and third ways require two steps. First, the two species could have evolved the trait independently. Secondly, all three species could have acquired the trait from a common ancestor, and one species subsequently lost it.

There are four synapomorphic characters in Table 3. Abdominal trophallaxis and absence of adult transport are shared by *Z. varians* and *P. scabriusculus* while absence of stridulation and of abdominal self-grooming are shared by *Z. varians* and *C. atratus*. Of the three possible cladograms using these four traits (Figure 2), two appear equally plausible. In both cladogram *A* and *B*, two of the four synapomorphies require two steps to generate the appropriate distribution of characters. Two steps means independent derivation of the characters, or common derivation and secondary loss. The third cladogram, *C*, can be rejected as unlikely by parsimony since all four synapomorphies require two steps to produce the appropriate pattern.

When the relative importance of characters is considered, cladogram *A* gains plausibility over *B*. The ability to stridulate has rarely been lost in the Myrmicinae (Markl, 1973). Therefore, a single loss (cladogram *A*) can be considered more likely than a double one (cladogram *B*). Similarly, abdominal grooming movements occur in almost all ants (Wilson, 1962; Farish, 1972); loss is probably a rare evolutionary event. The appropriate pattern of abdominal grooming is derived most parsimoniously in cladogram *A*. Adult transport (carrying) on the other hand is a character expressed to widely varying degrees among the ants. Nestmate carrying, used primarily during emigration to new nest sites, may be relatively easy to lose if it becomes unnecessary ecologically. The adult transport character then does not lend strong support to either cladogram. Finally, the appropriate pattern for abdominal trophallaxis is derived most parsimoniously in cladogram *B*. In cladogram *A*, *Cephalotes* loses this character secondarily. Since intraspecific abdominal trophallaxis rarely occurs in ants, and is poorly understood, the difficulty or ease of its subsequent loss cannot be evaluated. In summary, on the basis of a character by character evaluation, cladogram *A* is more plausible.

Implications for the Evolution of Worker Polymorphism

Monomorphism is the ancestral state of the worker caste in most ants and probably represents the ancestral state of the Cephalotini as well. In myrmicines, a few cases of secondary monomorphism are known in species with workers that are minute in comparison to the queen (Wilson, 1953, 1971). If worker monomorphism is accepted as the ancestral state in the Cephalotini, then cladogram *A* provides the most parsimonious derivation of the pattern of worker polymorphism. Cladogram *B* implies that the morphological worker caste systems characteristic of *Zacryptocerus* and *Cephalotes* evolved independently. According to cladogram *A*, the tendency to express morphological diversity within the worker caste evolved once. *Cephalotes* maintained a weak bimodality in the size frequency distribution over a wide size range (Corn, 1980), while the *Zacryptocerus* line intensified that bimodality, a trend which led to the completely dimorphic worker caste of some species.

If worker monomorphism is ancestral and *Procryptocerus* represents a relict state, it follows that, in the Cephalotini, soldiers must

be the primitive caste and minor workers the novel caste. In *Procryptocerus*, workers closely resemble the queen as do soldiers in *Zacryptocerus* and large workers in *Cephalotes*. Advanced cepalotines appear to have added smaller workers to their worker caste systems. Soldiers of *Zacryptocerus* fulfill the first of two criteria proposed in Wilson (1980) for a primitive caste: they resemble the workers of the less modified, monomorphic members of the same tribe (e.g. *Procryptocerus*). *Zacryptocerus* soldiers do not meet the second criterion, that the primitive caste perform the generalized services of a colony. Wilson (in press) has discovered that *Pheidole* soldiers can be induced to express behavior typical of a minor worker's repertoire; morphological specialization does not preclude behavioral flexibility. This discovery uncouples morphological and behavioral specialization and may relax the need for a primitive caste meeting the second criterion of generalized behavior.

Ecological Similarity

Ecological similarity between species can contribute significantly to similarities in behavioral traits. Cole has demonstrated that two species of ecologically similar but phylogenetically distant species of ants, *Z. varians* (Myrmicinae) and *Colobopsis* sp. (Formicinae) exhibit convergence of qualitative behavioral traits as well as of quantitative aspects of their repertoires. Both species inhabit hollow twigs of a variety of plants that represent dry habitats (Smith, 1923; Kempf, 1958; Cole, 1982).

Z. varians and *P. scabriusculus* are also ecologically similar. Both nest in hollow, dry twigs, and the ants themselves are of similar size. In *Z. varians*, minor workers measure 3.6–4.7 mm and soldiers 5.9–6.3 mm in total length (Kempf, 1958). The size of *P. scabriusculus* workers falls between the two castes of *Z. varians*, with workers measuring 4.6–5.2 mm in total length. The colony size of both species is also small, not exceeding several hundred workers. In addition, *Z. varians* is known to be nocturnal, and *P. scabriusculus* is believed to be nocturnal of crepuscular (Snelling, 1968).

C. atratus, in contrast, is a large ant (8–14 mm total length), nesting in spacious cavities in living wood. Colony size is extremely large compared to other cephalotines, with about 12,000 workers in a mature colony. They forage diurnally. Corn (1976) suggests that many of the differences between *C. atratus* and *Z. varians* might be based on the differences in nest site. Use of infrabuccal pellets as

food and high rates of regurgitation are adaptations to dry conditions (Wilson, 1976; Cole, 1980), and would not be necessary in *C. atratus* which nests in moist tree cavities (Corn, 1976). The relatively wide nest chambers of *C. atratus* may have provided an environment in which the primitive behavior of carrying nestmates was possible, and ultimately, retained (Corn, 1976). The lack of both infrabuccal pellets and abdominal trophallaxis may be indicative of an entirely different diet in *C. atratus* than either *P. scabriusculus* or *Z. varians*.

In summary, some of the behavioral similarities between *P. scabriusculus* and *Z. varians*, and the apparent divergence of *C. atratus*, may be based in ecology rather than phylogeny. Behavioral convergence of *P. scabriusculus* and *Z. varians* would lend further support to cladogram *A*.

Summary

P. scabriusculus is a cephalotine with multiple queens and a monomorphic worker caste. Differences in the behavior among individual queens suggest that queens are not equal in reproductive status. Newly emerged *P. scabriusculus* workers indulge in prolonged periods of abdominal trophallaxis. Abdominal trophallaxis has been reported previously in *Z. varians*, an advanced cephalotine with a dimorphic worker caste. Cladograms based on behavioral characters support a phylogenetic scheme in which the divergence of *Procryptocerus* occurred prior to the divergence of *Cephalotes*. Within the Cephalotini, the minor workers, rather than soldiers, appear to be the novel worker caste.

Acknowledgements

I would like to thank all the Eberhards for encouraging me to work in Costa Rica and for making this study not only possible but pure pleasure. L. Freed helped me locate, and provided transportation to cephalotine habitats in Panama. I thank N. F. Carlin, D. S. Gladstein, and R. M. Fagen for guiding the analysis of the repertoire and W. P. Maddison for enlightening discussions of cladistics. N. F. Carlin, B. Hölldobler, W. P. Maddison, and E. O. Wilson provided constructive comments on earlier versions of the manuscript. Funds were provided by a Smithsonian Postdoctoral Fellowship and NSF Grant #PCM-8301763.

Literature Cited

Brandao, C. R. F.

1978. Division of labor within the worker caste of *Formica perpilosa* Wheeler (Hymenoptera: Formicidae). Psyche **85**: 229–237.

1983. Sequential ethograms along colony development of *Odontomachus affinis* Guerin (Hymenoptera, Formicidae, Ponerinae). Insectes Soc. **30**: 193–203.

Brown, W. L.

1973. A comparison of the Hylean and Congo-West African rain forest fauna. In Tropical Forest Ecosystems: a comparative review. B. J. Meggers, E. S. Ayensu and W. D. Duckworth, Eds. Smithsonian Institution Press, Washington, pp. 161–185.

Bulmer, M. G.

1974. On fitting the Poisson lognormal distribution to species-abundance data. Biometrics **30**: 101–110.

Carlin, N. F.

1981. Polymorphism and division of labor in the dacetine ant *Orectognathus versicolor* (Hymenoptera: Formicidae). Psyche **88**: 231–244.

Cleveland, L. R.

1926. Symbiosis among animals with special reference to termites and their intestinal flagellates. Q. Rev. Biol. **1**: 51–60.

Cole, B. J.

1980. Repertoire convergence in two mangrove ants, *Zacryptocerus varians* and *Camponotus* (Colobopsis) sp. Insectes Soc. **27**: 265–275.

1982. The guild of sawgrass-inhabiting ants in the Florida Keys. Psyche **89**: 351–356.

Corn, M. L.

1976. The ecology and behavior of *Cephalotes atratus*, a Neotropical ant (Hymenoptera: Formicidae). Ph.D. Dissertation. Harvard University.

1980. Polymorphism and polyethism in the Neotropical ant *Cephalotes atratus* (L.). Insectes Soc. **27**: 29–42.

Creighton, W. S.

1963. Further studies on the habits of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). Psyche **70**: 133–143.

1967. Studies on free colonies of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). Psyche **74**: 34–41.

Creighton W. S. and R. E. Gregg.

1954. Studies on the habits and distribution of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). Psyche **61**: 41–57.

Creighton, W. S. and W. L. Nutting.

1965. The habits and distribution of *Cryptocerus rowheri* Wheeler. Psyche **72**: 59–64.

Eisner, T. and G. M. Happ.

1962. The infrabuccal pocket of a formicine ant: a social filtration device. Psyche **69**: 107–116.

EMERY, C.
1888. Uber den sogenannten Kaumagen einiger Ameisen. Z. wiss. Zool. **46:** 378-412.

FAGEN, R. M.
1978. Repertoire analysis. In *Quantitative Ethology*. P. W. Colgan, Ed. John Wiley and Sons, New York.

FAGEN, R. M. AND R. N. GOLDMAN.
1977. Behavioral catalogue analysis method. Anim. Behav. **25:** 261-274.

FARISH, D. J.
1972. The evolutionary implications of qualitative variation in the grooming behaviour of the Hymenoptera (Insecta). Anim. Behav. **20:** 662-676.

HASKINS, C. P. AND E. V. ENZMANN.
1938. On the occurrence of certain sociological and physiological features in the Formicidae. Ann. N. Y. Acad. Sci. **37:** 97-162.

HENNIG, W.
1966. Phylogenetic systematics. University of Illinois Press, Urbana, Illinois.

HÖLLDOBLER, B. AND E. O. WILSON.
1977. The number of ant queens: An important trait in evolution. Naturwiss. **64:** 8-15.

KEMPF, W.
1951. A taxonomic study on the ant tribe Cephalotini. Rev. Entomol. **22:** 1-244.
1958. New studies of the ant tribe Cephalotini (Hym. Formicidae). Studia. Entomol. **1:** 1-176.
1972. Catalogo abreviado das formigas das regiao Neotropical (Hymenoptera: Formicidae). Studia Ent. **15:** 3-344.
1973. A new *Zacryptocerus* from Brazil, with remarks on the generic classification of the tribe Cephalotini (Hymenoptera: Formicidae). Studia Ent. **16:** 449-462.

LIMONGI, J.
1977. Variacion de tamaños en la poblacion de *Zacryptocerus pusillus* en los llanos venezolanos. Smithsonian Tropical Research Institute. Exxon Student Reports.

MARKL, H.
1965. Stridulation in leaf-cutting ants. Science **149:** 1392-1393.
1973. The evolution of stridulatory communication in ants. Proc. 7th Congr. IUSSI, London: 258-265.

MARKL, H. AND B. HÖLLDOBLER.
1978. Recruitment and food-retrieving in Novomessor (Formicidae, Hymenoptera). II. Vibration signals Behav. Ecol. Sociobiol. **4:** 183-216.

MASTERS, W. M.
1979. Insect disturbance stridulation: its defensive role. Behav. Ecol. Sociobiol. **5:** 187-200.

MÖGLICH, M. AND B. HÖLLDOBLER.
1974. Social carrying behavior and division of labor in ants. Psyche **81:** 219-236.

SHARP, D.
1893. On stridulation in ants. Trans. Entomol. Soc. Lond. 1893, p. 199–213.
SMITH, M. R.
1923. Two new Mississippi ants of the subgenus Colobopsis. Psyche **30**: 82–88.
SNELLING, R.
1968. Taxonomic notes on some mexican cephalotine ants (Hymenoptera: Formicidae). L. A. Co. Mus. Contrib. Sci. **132**: 1–10.
STUART, R. J.
1981. Abdominal trophallaxis in the slave-making ant, *Harpagoxenus americanus* (Hymenoptera: Formicidae). Psyche **88**: 331–333.
TAYLOR, R. W.
1978. *Nothomyrmecia macrops*: A living ant fossil. Science **201**: 979–985.
TRANIELLO, J. F. A.
1982. Population structure and social organization in primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). Psyche **89**: 65–80.
WEBER, N. A.
1957. The nest of an anomalous colony of the arboreal ant *Cephalotes atratus*. Psyche **64**: 60–69.
WHEELER, G. C. AND J. WHEELER.
1954. The ant larvae of the myrmicine tribes Cataulacini and Cephalotini. J. Wash. Acad. Sci. **44**: 149–157.
WILSON, E. O.
1953. The origin and evolution of polymorphism in ants. Q. Rev. Biol. **28**: 136–156.
1962. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. Bull. Mus. Comp. Zool. (Harvard) **127**: 401–422.
1971. *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, Mass.
1974. Aversive behavior and competition within colonies of the ant *Leptothorax curvispinosus*. Ann. Entomol. Soc. Am. **67**: 777–780.
1975. *Leptothorax duloticus* and the beginnings of slavery in ants. Evolution **29**: 108–119.
1976. A social ethogram of the Neotropical arboreal ant *Zacryptocerus varians* (Fr. Smith). Anim. Behav. **24**: 354–363.
1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens*. Behav. Ecol. Sociobiol. **7**: 143–156.
1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae. Behav. Ecol. Sociobiol. (in press).
WILSON, E. O. AND R. M. FAGEN
1974. On the estimation of total repertoire size in ants. N. Y. Entomol. Soc. **82**: 106–112.